

Radio tracking detects behavioral thermoregulation at a snail's pace

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ABSTRACT

The dynamic ebb and flood of tides makes the marine intertidal zone a habitat with temperatures that fluctuate rapidly in both space and time. This is problematic for slow intertidal organisms that cannot move at the speed of tidal fluctuations. The timing of low tides determines which days organisms may experience extreme body temperatures, controlling microclimate to a greater degree than weather patterns. When low tides occur midday, temperatures can exceed critical thermal maxima for many species. Although high shore areas experience the greatest environmental extremes, they often harbor untapped food resources. The periodicity of low tide timing creates a predictable cycle that marine animals can use to obtain food in risky areas while minimizing exposure to thermal extremes. Here, we use a two-part approach to assess whether the snail, *Nucella ostrina*, uses the predictability of the tidal cycle to obtain food in risky areas while minimizing exposure to thermal extremes. Radio tracking detected the presence/absence of snails in high shore feeding areas continuously for 14 weeks and physical thermal models approximated snail body temperature in those high shore areas. Snails were absent when extreme low tides occurred at times of high solar irradiance (midday). Comparing the subset of physical model body temperatures foraging snails experienced to all available body temperatures in the high shore environment showed snails in foraging areas disproportionately at 9–12 °C and absent at body temperatures > 31 °C, suggesting that *N. ostrina* is not present when and where thermal risk is greatest. These patterns demonstrate that censusing only at low tide yields an adequate picture of foraging behavior of this species in its natural habitat, and that migratory foraging behavior effectively moderates snail experience of environmental temperature in nature and may buffer this species from aerial warming.

1. Introduction

An animal's behavior modifies how it experiences its environment and can act as a filter of undesirable conditions (Buckley et al., 2013; Huey, 1991; Kearney et al., 2009; Lathlean, 2014; Sears et al., 2016; Sunday et al., 2014), therefore altering the temporal and spatial scales at which a species will be affected by climate change (Deutsch et al., 2008; Kearney et al., 2009; Sears et al., 2011; Woods et al., 2015). Correctly accounting for animal behavior is critical to relating environmental conditions to performance and risk in a changing world.

Organisms inhabiting marine intertidal zones are subjected to potentially stressful physical conditions whenever tides retreat. When the tide is low on warm, sunny days, organisms have a high risk of exposure to temperatures exceeding thermal maximums. Mobile intertidal organisms may change their behavior drastically to minimize thermal risks, for example, actively selecting thermally favorable microsites (Chappon and Seuront, 2011a) or changing body orientation to regulate heat gain (Munoz et al., 2005). Intertidal zones have a gradient of

thermal and desiccation stress: higher shore elevations are exposed to air for longer than lower elevations and therefore are more likely to reach high temperature and low humidity extremes. Mobile intertidal animals must choose between seeking food in exposed high shore areas that are accessible only to the most physiologically robust species (Connell, 1970), or taking refuge in cracks and lower on shore where food stocks may be depleted by competitors (Johnson et al., 1998). Organisms are constrained by the distance between high and low intertidal elevations, up to several meters in many systems, and by potential water loss if moving when emerged at low tide or across dry substrates. Fast organisms move into new foraging areas with a flooding tide and retreat with the receding tide (Holsman et al., 2006; Yamada and Boulding, 1996). For example, small shore crabs can run over ground up to 1.4 m s⁻¹ (Martinez, 2001). The much slower locomotion and feeding of animals such as snails suggests they must adopt a different mechanism of balancing foraging with risk avoidance.

Thermal complexity created by tidal cycling controls benthic environmental conditions more than any climatic factor, creating a

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variety of microhabitats (Mislán et al., 2009). Low tide aerial exposure varies seasonally and geographically, occurring at different times of day. However, within season and location tidal patterns repeat on a two-week interval. Aerial exposure during midday subjects intertidal organisms to higher solar radiation, and therefore body temperatures, than they experience when low tide occurs at other times of day (Hayford et al., 2015; Helmuth et al., 2002). The air temperature may or may not be high on any given day, yet it can only reach maximum values on days with long midday low tides. This makes the two-week tidal cycle a potentially dependable feature of a stochastic environment. Tidal phase (high or low, ebb or flood), day-night, and seasonal cycles have often been considered in assessment of thermoregulatory behavior in tidal invertebrates (for example Garrity, 1984; Harper and Williams, 2001; Little, 1989; Takada, 1996). Less common are connections between the two-week tidal cycle and thermal risk (but see Burrows and Hughes, 1989; Moran, 1985; Spight, 1982), yet the two-week periodicity creates spatio-temporal thermal variation which may provide reliable cues for tidal organisms.

Slow intertidal animals can take advantage of both food and thermal refuge if they are selective in their foraging timing. Risk is reduced on days when low tides are timed such that most aerial exposure is at night or early in the morning (Hayford et al., 2015). It is therefore predicted that slow mobile organisms are most active in the high shore region on those days of the tidal cycle with minimal midday aerial exposure.

Nucella ostrina (Gould, 1852) is a predatory snail common to intertidal shores throughout the Northeast Pacific. In the San Juan Islands, Washington, USA, *N. ostrina* feeds preferentially on the barnacle *Balanus glandula* (Connell, 1970). *N. ostrina* forages at all tidal heights when barnacle prey are available, however, prey at lower shore elevations are typically consumed by superior competitors of *N. ostrina* in the spring or early summer. By late summer the remaining available prey are located high on shore. The process of crawling (1.3 cm min^{-1} for a typical individual, data not shown), selecting, drilling, and ingesting a prey item ($5.3 \pm 0.37 \text{ h}$ for drilling and ingesting an average sized barnacle) can exceed 24 h and typically takes longer than the duration of a high tide (Emlen, 1966). In experimental tests using caged snails in the laboratory and field (Vaughn et al., 2014 and Hayford et al., 2015, respectively), snails moved into exposed areas in the high intertidal during days of the two-week tidal cycle when thermal and desiccation risk were reliably low, and foraged for multiple consecutive days before retreating to thermal refuges (Fig. 1). Snails selected days of the tidal cycle when foraging areas were subject to reduced potential sun exposure. However, these manipulated conditions offered a dichotomous choice of food or refuge within a few cm of one another, and so only provided suggestive evidence of how snails behave in more heterogeneous natural habitats. Sampling only at low tide would have

missed *N. ostrina* movement into high shore areas during high tides. Furthermore, measuring habitat temperatures likely wasn't as accurate an assessment of thermal risk as estimating body temperature (Gilman et al., 2006; Helmuth, 1998; Helmuth and Hofmann, 2001).

The objectives of this study were to determine whether: (1) natural populations of *Nucella ostrina* forage periodically as has been previously observed in experimental manipulations; (2) snail foraging behavior limits thermal risk; and (3) censusing only at low tide provides an adequate picture of snail foraging behavior. We predicted that *N. ostrina* would forage only on the few days of the two-week tidal cycle when the chances of high temperatures were reduced by timing of tidal cycling, thereby reducing thermal risk to the snail, and that surveying only at low tide would adequately assess snail populations if surveys were conducted on foraging days.

2. Materials & methods

2.1. Low tide surveys of microhabitat use

The intertidal snail *Nucella ostrina* was tracked to assess habitat use in nature and whether behavior moderated thermal experience within the wide range of natural thermal heterogeneity. Typically < 3 cm in length, *N. ostrina* is too small to carry a traditional temperature logger. Instead, a two-part approach was used: tracking with radio frequency identification (RFID) tags and estimating operative body temperature with physical thermal model loggers that approximated body temperature of live organisms. Snail censuses were conducted at multiple sites on the University of Washington Friday Harbor Laboratories Research Preserve (FHL, 48°33' N, 123°00' W) on San Juan Island, Washington, USA. The mean tidal range (difference between mean higher high water, MHHW, and mean lower low water, MLLW) for this NOAA station (#9449880, www.tidesandcurrents.noaa.gov) is 2.36 m, with a lowest recorded water level of -1.27 m and highest water level of 3.40 m , relative to MLLW. Observed water levels and physical thermal model temperatures were used to assess the relationship between snail behavior, estimated body temperature, and tidal emersion. Three intertidal sites, separated from one another by approximately 100 m alongshore distance, were selected for their relatively steep, east-facing rock surfaces. This semi-vertical substrate was chosen from a variety of available substrate aspects because it decreased the horizontal distance that an animal would have to travel to change tidal elevation. Each site consisted of a rectangular census plot stretching 1.0 m alongshore and vertically from 1.0 m above mean lower low water (MLLW) to 2.25 m above MLLW, plus a larger RFID search area. Epoxy markers (#788, Z-spar Coatings, Kop-Coat, Inc., Rockaway, New Jersey, USA) were used to semi-permanently mark plots. RFID search areas consisted of the heterogeneous rocky region of approximately 20 m^2 surrounding each plot. These included horizontally and vertically-oriented surfaces, and were bounded by natural features such as crevices, which were included in searches. The total count of snails in each census plot plus any individual with an RFID tag in the surrounding search area was determined daily and averaged across all three sites. RFID tags enabled individuals to be detected even when they were in microhabitats with low visibility. Each snail was assigned a bivariate level of solar exposure: unprotected from sun (exposed) or in cracks or under algal canopy (refuge), microhabitats known to be cooler on this shoreline (Gilman et al., 2015); and a bivariate vertical tidal elevation: below 1.5 m (low shore) or 1.5 m or above (high shore). This elevation corresponds with the approximate peak barnacle density, yet is above mean elevation for the snails at these sites.

RFID tags (12 mm HDX + PIT, Oregon RFID, Portland, Oregon, USA) were affixed to the shells of *N. ostrina* that naturally occupied chosen survey sites and were 2 cm or greater in shell length (Supplemental Fig. S1). Half duplex (HDX) tags are resistant to electrical noise which allows for the transmission of radio signal through highly-conductive seawater and therefore the tracking of snails while

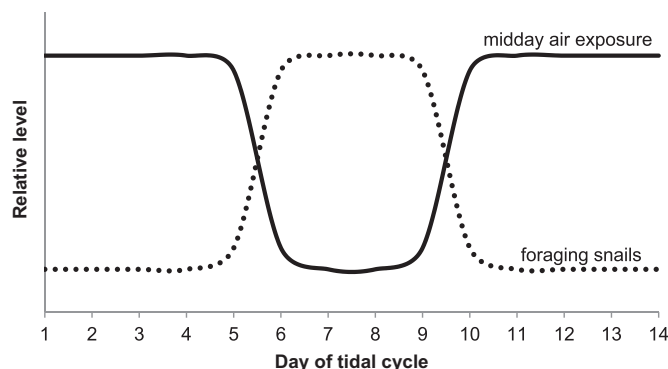


Fig. 1. Conceptual model of snail behavior during a two-week tidal cycle. Midday aerial exposure (solid line) changes throughout the cycle due to low tide timing. The proportion of snails on a given shoreline that forage in sun-exposed, high-shore locations (dotted line) increases on those days of the tidal cycle where midday aerial exposure is minimized.

submerged. Recent advances in the construction of HDX tags allow manufacture at sizes appropriate for use on small marine invertebrates. Snails were collected, tag was affixed to the dorsal region of the shell with Z-spar marine epoxy, and snails were returned during one low tide period. The days of a two-week tidal cycle when *N. ostrina* would forage at high tidal elevations were predicted to be those with the fewest minutes of midday air exposure, based on prior observations (Hayford et al., 2015; Vaughn et al., 2014). A total of 23 snails were tagged with RFID: 6–10 individuals at each site. To compare survey efficiency to traditional visual methods and determine whether RFID tags altered snail behavior, an additional 20 total snails were marked with numbered wire tags (WireMarkerBooks.com, Brooklyn, New York, USA). Each site was scanned by eye during low tide for the presence of visual tags and using a handheld tag reader with an attached wand antenna (APR 350 with AEA 580, Agrident GmbH, Barsinghausen, Germany) for radio tags.

Daily surveys were conducted over a two-week tidal cycle, August 6, 2012 to August 19, 2012. Previous observations indicate this is a season when fluctuations in substrate temperature are large (7.8–40.2 °C in 2011, data not shown) and *N. ostrina* density is great in high shore areas (Connell, 1970). Additionally, opportunistic surveys were conducted June 19, 2012 through August 30, 2012 to determine RFID detection efficiency relative to visual tags. Changes in distributions of snails from one day to the next were assessed by Generalized Linear Mixed Modeling (GLMM, Table 1). GLMM allowed calculation of probability with spatially and temporally correlated data and incorporated a binomial distribution of error terms to account for a binary response variable (Bolker et al., 2009). In each test, the hypothesized model was compared to a null model that included only an intercept and random factor. Chi-square Goodness of Fit test was used to determine whether the hypothesized model fit data better than the null, as in Lowe et al. (2015). Two different response variables were tested as a function of fixed factor, day of tidal cycle, and random factor, survey site; first, snail use of habitat, either in refuge or exposed, and second, snail elevation, high (≥ 1.5 m) or low (< 1.5 m), on shore. Fitted models were checked for overdispersion by comparing the ratio of the Chi-square distribution of the full model residuals to the residual degrees of freedom using the overdispersion function provided by Bolker et al., 2009 (<http://bbolker.github.io/mixedmodels-misc/glmmFAQ.html#overdispersion>). The relationship between snail use of habitat and the potential tidal cue, change in duration of midday aerial exposure due to low tide, was assessed by linear regression. The daily proportion of snails in high shore areas (≥ 1.5 m) versus all snails found on that day was averaged across sites and regressed to the change in minutes of midday low tide aerial exposure (within 3 h of solar noon) since the previous day. Similarly, the mean daily proportion of snails in sun-exposed areas was compared to the change in minutes of midday low tide aerial exposure. Statistical tests were performed in Rv. 3.1.3 (R Core Team, 2015) with package lme4 (Bates et al., 2015).

2.2. Continuous remote tracking

The behavior of free-range intertidal snails was explored through

Table 1

Summary of linear model statistics.

Generalized linear mixed modeling (GLMM) with a binomial distribution of error terms was used to assess snail distribution in refuge versus exposed habitats and distribution above or below 1.5 m shore elevation. Bold p-values highlight probabilities < 0.05 .

Response	Model	Error	AIC	χ^2	df	p
Snail habitat	1: habitat ~ day + (1 site)	Binomial	981.5	173.0	13	< 0.001
	2: habitat ~ 1 + (1 site)	Binomial	1128.5			
Snail elevation	1: elevation ~ day + (1 site)	Binomial	1202.6	20.9	13	0.074
	2: elevation ~ 1 + (1 site)	Binomial	1197.5			

two different uses of radio frequency identification (RFID) tags: (1) low tide field surveys locating the same individuals on subsequent days by tracking tags using a hand-held device; and (2) continuous remote tracking detecting tags in one sun-exposed, high shore location throughout both high and low tides.

Antennas at two elevations at one FHL site scanned for tags continuously from August 15, 2013 to November 23, 2013 (14 weeks). Antennas encircled high shore areas with barnacle prey present, but few topographical or biological thermal refuges (Fig. 2). These areas were termed “exposed,” referencing their lack of protection from solar radiation. Antennas scanned for RFID tag signals continuously, recording tag detections to a data logger when a snail crossed into the range of the antenna (typically 1–15 cm, depending on tag angle).

Antennas were constructed of stranded tin-copper wire (20 AWG, Newark element14, Chicago, Illinois, USA), turned in 5 consecutive oblong loops of 15 cm by 1.1 m (inductance 50 μ H). Antennas were installed with the long axis of the loop horizontal at 1.5 m and 2.0 m above MLLW with marine epoxy (Splashzone Epoxy #788, Z-spar Coatings, Kop-Coat, Inc., Rockaway, New Jersey, USA). Snails could crawl over the wire as well as under in some places. Snail tags were within 1 cm of antenna loop when snails were crossing, however read range variability affected whether snails in the center of the loop were continually detected.

Antenna tuner boards (Slim Tuning Capacitors, Oregon RFID, Portland, Oregon, USA) delivered charge to the wire loops at the correct frequency. Tuner boards were waterproofed using modified methods of Bond et al. (2007). Mini-buccaneer connectors (Bulgin, Cambridge, England, UK) were soldered to tuner boards, then tuner boards were potted in electronics resin (Sealtronic 21AC, System Three, Auburn, Washington, USA). Twinaxial cables ran from tuner boards 10 m up-shore to a data logger (Multi-Antenna HDX Reader, Oregon RFID, Portland, Oregon, USA) housed onshore and connected to AC power. In the field, tuner boards and cables were bolted into the rock. The data logger was set to a scan rate of 0.95 Hz (50 ms charge period and 1000 ms listen period).

Sixty-two *N. ostrina* individuals were tagged over the 4 months prior to the beginning of the remote detection study and another 5 tags were added throughout the survey period as new snails were found in survey regions, for a total of 67 individuals. Each antenna detects only one tag signal at a time. Whereas in many applications the organism, such as a salmon, passes through the antenna read range within a matter of seconds, slow-moving benthic snails may spend several consecutive hours within read range of the antenna, essentially jamming the system. Limiting the density of tagged organisms by selecting a site without high snail density (< 5 individuals m^{-2}) therefore reduced the likelihood of missing a detection due to interference between tags. Early tests with antennas mounted in an aquarium tank failed to detect antenna crossings of tagged *N. ostrina* only when two or more individuals were in read range of the antenna at one time.

Tagged individuals in the study area decreased over time, presumably due to snails moving out of the survey area or to death. Snails were presumed to be continuously occupying areas adjacent to antennas when the duration of time between subsequent detections for a

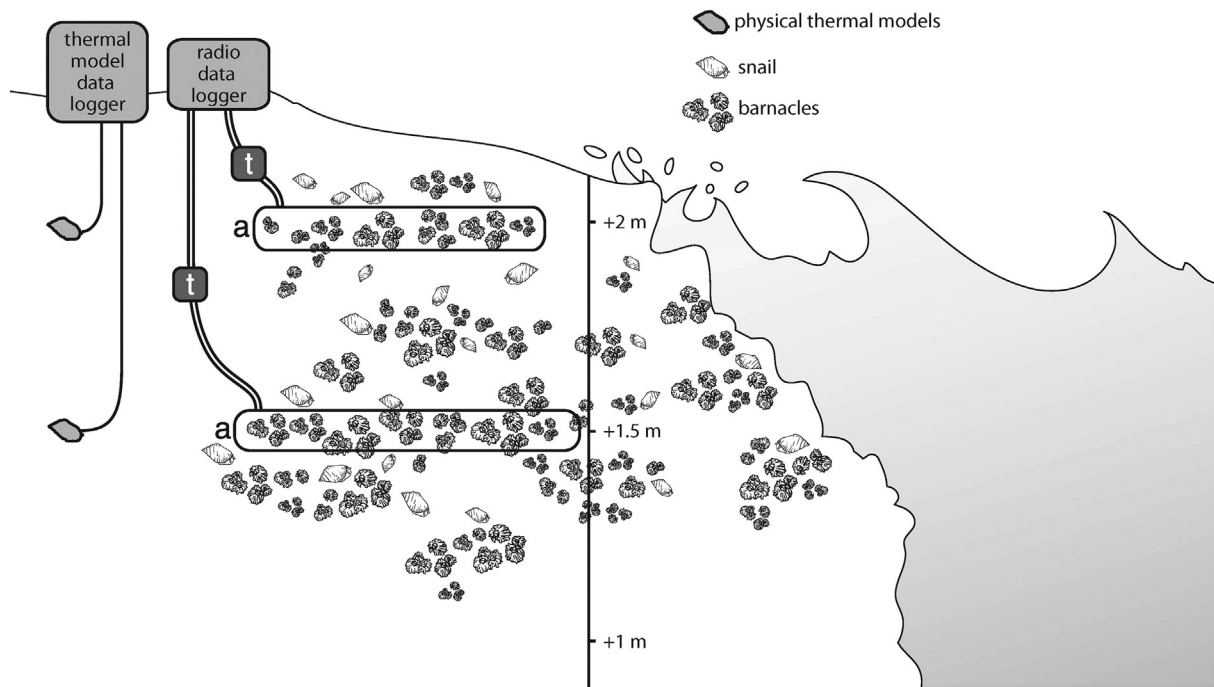


Fig. 2. Schematic of radio antennas and physical thermal models mounted to the intertidal shoreline.

Movement and temperature of the snail, *Nucella ostrina*, as it preyed upon the barnacle, *Balanus glandula*, was monitored using a two-part system: (1) radio frequency identification (RFID), consisting of RFID-tagged snails, antenna wire loops (a), antenna tuners (t), shielded wire (double line), and radio data logger; (2) temperature, consisting of thermocouple wires (fine line), physical thermal models, and thermal model data logger. Systems were placed adjacent to each other at two tidal elevations, 1.5 and 2.0 m above mean lower low water (MLLW, 0 m). In the late summer and autumn, low shore barnacles had been consumed and available prey density was highest in high shore regions.

given tag was < 24 h. This value was chosen to overestimate the range of body temperatures that snails might experience when present in high shore areas, a conservative approach to evaluating snail behavior in thermal extremes. To verify that snails were absent from sun-exposed high shore areas when there were no detections, daily surveys were conducted using a hand scanner and antenna (as above) from August 19, 2013 to September 21, 2013 (4.5 weeks). Only one incident of false negative was found: four undetected snails were in the antenna area on August 20, 2013.

Tidal cycling regimes shift in the spring and autumn each year. At FHL, lower low tides occur during midday in the spring and summer (until mid-September) and at night in the autumn and winter. Therefore, time series analysis of estimated body temperature and of snail count in high shore areas measured across the seasonal shift in tidal regime were not expected to yield significant periodicity. These patterns were tested using autocorrelation (ACF) with significance assigned to correlation coefficients outside the 95% confidence intervals.

2.3. Thermal consequences of movements

Physical thermal models were constructed to closely approximate body temperature of *N. ostrina* in its environment ($\pm 3^\circ\text{C}$), following the design of Gilman et al. (2015). Thermal models were created from the shells of deceased *N. ostrina* (length 2.0–2.5 cm), with one end of a thermocouple embedded at the apical end of the shell and filled with Two Ton Epoxy (Devcon, Danvers, Massachusetts, USA). Thermal models were wired to a multiplexer (25 T and CR1000, Campbell Sci, Logan, Utah, USA) logging model temperature every 15 min. Wires were secured with wire clips and screws drilled into the rock. A thermal model was affixed to the substrate with Z-spar marine epoxy in unshaded portions of the south-facing rock, adjacent to each high shore antenna (Fig. 2). A 3-year study of summer temperatures of physical thermal models had demonstrated that shore elevation and microclimate were more important than morphology (species) in determining estimated body temperature, with low shore and refuge areas

consistently cooler than high shore exposed areas (Gilman et al., 2015). The relationship between duration of midday aerial exposure due to low tide and daily maximum temperature of the thermal models was evaluated by linear regression.

A single physical thermal model adjacent to each antenna was used to approximate the body temperature *N. ostrina* would experience if present in that location. The physical thermal model at 1.5 m was compared to a duplicate model for 5 weeks (August 15, 2013 to September 22, 2013) with a mean difference of $\pm 0.12^\circ\text{C}$. This suggests greater variation between a physical model and a live snail than between models at a given tidal elevation. A subset of model temperatures including only those data taken when a snail was present in the adjacent antenna was used to estimate the body temperature experienced by any snail (T_s) migrating through these locations.

Estimated body temperatures experienced by migrating snails in foraging areas (T_s) observed through continuous remote tracking were compared to all estimated body temperatures available in the environment (T_e) by resampling from the full pool of measured T_e values, a technique similar to bootstrapping. Resampling was performed in base R as follows. A sample size equivalent to the subset T_s ($n = 2343$) was randomly drawn from the full data set T_e ($n = 19,200$) without replacement. We were concerned that if a smaller range of temperatures was found for T_s , it would be an artefact of drawing a small subset of temperatures from a larger set (akin to a finite population). We resampled without replacement to determine whether drawing a small subset from our temperature population typically resulted in a reduced temperature range. The maximum and minimum values of the random draw were calculated for 10,000 iterations. The range of values of T_e was considered to be significantly larger than that of T_s if the 95% CI for the maximum and minimum of resampled T_e values exceeded the maximum and minimum of observed T_s . Similarly, the percent of records in the range 9–12 $^\circ\text{C}$ was calculated for each of 10,000 resamples ($n = 2343$ in each resample). Snails were considered to have spent significantly more time in this range of estimated body temperatures than by chance alone if the percent of T_s 9–12 $^\circ\text{C}$ fell outside the 95% CI

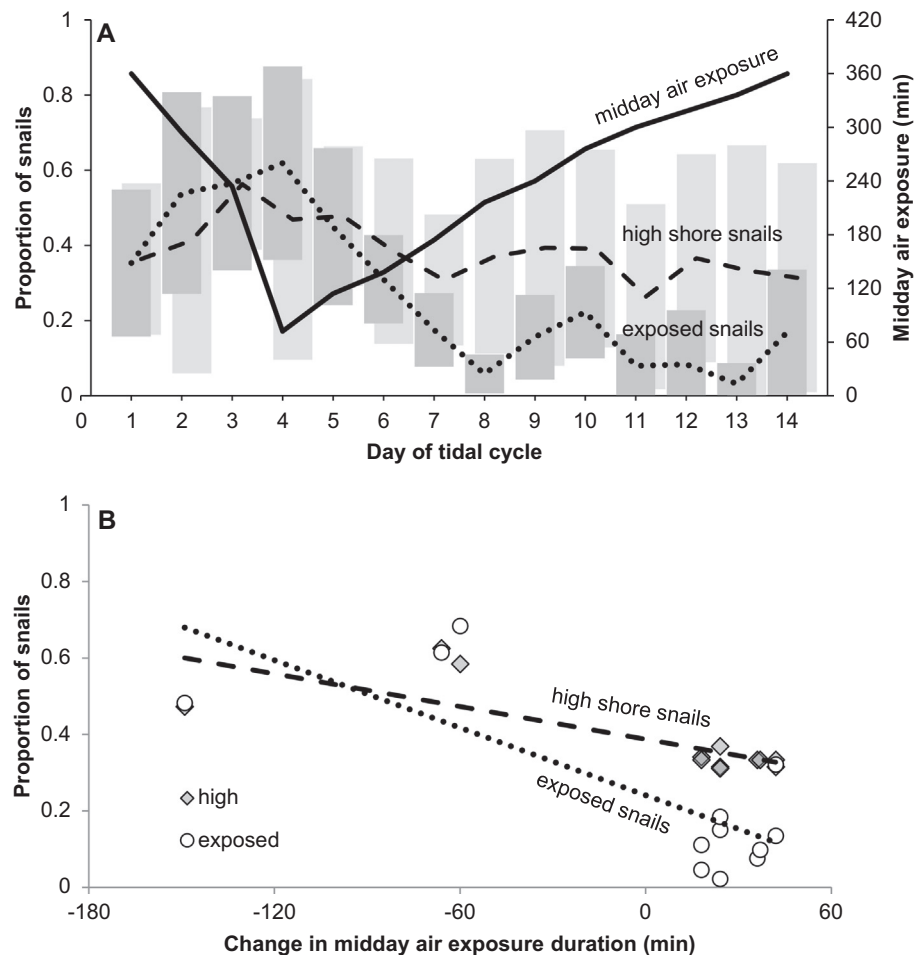


Fig. 3. Distribution of snails in relationship to low tide aerial exposure.

Daily distribution of snails over two-week tidal cycle in August, 2012. *Nucella ostrina* present at three intertidal sites or in the surrounding 20 m² search area on the Friday Harbor Laboratories Preserve over a 14-day tidal cycle, beginning August 6, 2012. At each site a 1 m horizontal band was surveyed from 1 m above mean lower low water (MLLW) to 2.25 m above MLLW. (A) Mean proportion in fully sun-exposed locations (dotted line) and on the high shore from 1.5 m to 2.25 m above MLLW (dashed line). Shaded bars, slightly offset for visualization, mark standard deviation of proportion of snails in sun-exposed locations (dark gray) and proportion of snails on the high shore (light gray). Duration of midday aerial exposure (min) due to tide below 1.5 m, defined as low tides occurring within 3 h of solar noon (solid line) is plotted on secondary axis. Midday aerial exposure occurring within 3 h of solar noon is minimal day 3–6 and maximal days 1 and 12–14. (B) Mean proportion in fully sun-exposed locations (circles, dotted line, $R^2 = 0.607$, $p = 0.001$) and on the high shore from 1.5 m to 2.25 m above MLLW (diamonds, dashed line, $R^2 = 0.572$, $p = 0.002$) in relationship to the change in duration of midday air exposure since the previous day. See Sections 2.1 and 3.1 for details.

of the mean proportion of resampled temperatures.

3. Results

3.1. Low tide surveys of microhabitat use

Radio tags were found to be an order of magnitude more efficient for relocating an organism than the traditional method of marking with a visual tag. Of an initial 20 visual tags and 23 RFID tags, 27 visual and 253 RFID detections were cumulatively made within the same search time. Not all detected RFID tags could be visually located. RFID tags allowed assessment of the habitat of individual snails by enabling a greater number in cracks to be found, thus better characterizing refuge use. Sixteen of the 23 tags (70%) were detected at least once following initial tagging. Eleven of 23 tags were detected during the 2 weeks of daily habitat and elevation surveys (Supplementary Fig. S2).

There was a greater number of *Nucella ostrina* in exposed high shore areas on certain days of the two-week tidal cycle, possibly the result of both snails moving out of adjacent refuge areas and moving up shore (Fig. 3). Over time, snails were not evenly distributed in exposed and refuge areas ($p < 0.001$, Table 1). Although refuges, such as cracks and algal canopies, were used throughout the two-week survey, the proportion of snails in exposed areas greatly increased on days 3–5 of the tidal cycle (Fig. 3A).

Nucella ostrina changed elevation throughout the two-week tidal cycle, although this trend was not statistically significant at the $\alpha = 0.05$ level ($p = 0.074$, Table 1, Fig. 3A). Increases in mean count were largely driven by increases high on shore (≥ 1.5 m), while snail numbers below 1.5 m tidal elevation were relatively consistent over a

biweekly tidal cycle. Importantly, the greatest proportion of snails in the high shore regions were observed during the 3 days predicted to be foraging peaks by the tidal conditions (Hayford et al., 2015)—those days with the shortest duration of midday aerial exposure (Fig. 3A).

When low tide duration increased from the previous day, the mean proportion of snails in the high shore (1.5 m to 2.25 m above MLLW) was lower than on days when the low tide duration had decreased ($R^2 = 0.572$, $p = 0.002$, Fig. 3B), as was the mean proportion of snails in fully sun-exposed locations ($R^2 = 0.607$, $p = 0.001$, Fig. 3B).

3.2. Continuous remote tracking

A total of 811 tag detections for *N. ostrina* were received during the course of antenna deployment, representing 23 different tags or a 34% recapture of the 67 tags deployed. Twenty-one tags were detected > 1 week and 15 were detected > 4 weeks after tagging. Over the 14 weeks survey period (98 days), *N. ostrina* ventured into the 1.5 m exposed region frequently (on 52 days) and into the 2.0 m exposed region on rare occasions (3 days). 56.5% of the time snails were detected in exposed high shore areas when those areas were submerged by seawater. Snails ventured into exposed high shore areas on days of the tidal cycle that had reduced periods of midday (within 3 h of solar noon) aerial exposure and reduced daily maximum estimated body temperature (T_{\max} , Fig. 4). A seasonal decrease in air temperature was observed such that no T_{\max} exceeded 25 °C after October 22, 2013.

Snails did not regularly make brief excursions into high shore areas at high tide. We observed only two incidences of an individual moving from the 1.5 m into the 2.0 m area and retreating within the course of a high tide. Each organism was detected for < 2 h at the 2.0 m elevation.

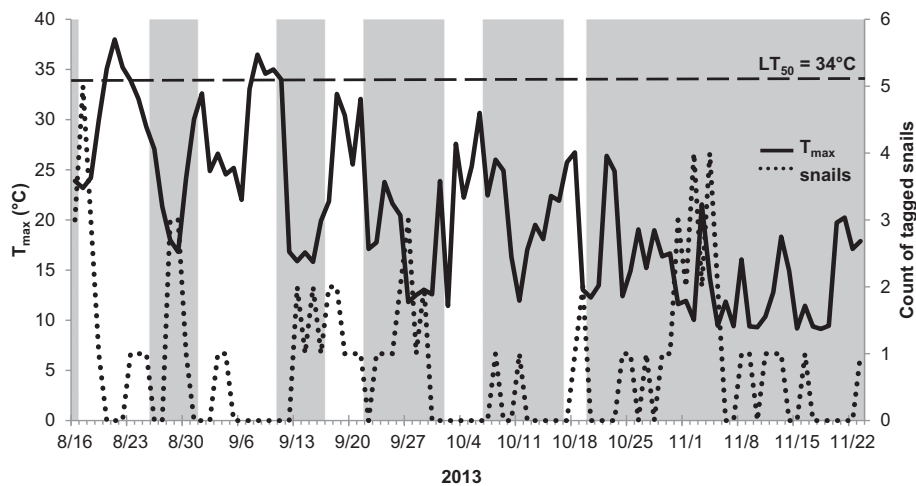


Fig. 4. Snails absent on days with high maximum temperatures in autumn 2013.

Maximum daily temperature of physical thermal model in high shore zone (solid line) and count of tagged snails detected by continuous radio monitoring in high shore areas (dotted line) over 14-week sampling period from August to November 2013. Dashed line marks LT_{50} of *Nucella ostrina*, 34 °C, based on Bertness and Schneider (1976). Days with fewer than 180 min of midday aerial exposure (occurring within 3 h of solar noon), representing days with reduced thermal risk, are shaded in gray.

Tag detections were sporadic, consisting of different members of the population, though several individuals made repeat visits to antenna areas, including after several weeks of absence. As expected during the seasonal switch of tidal regime, neither T_{max} of thermal models nor snail count exhibited significant two-week periodicity (Supplemental Fig. S3).

3.3. Thermal consequences of movements

Duration of aerial exposure due to low tides had a strong positive influence on daily T_{max} of thermal models ($R^2 = 0.533$, $p < 0.001$, Fig. 5). Spring and neap tide designations did not characterize aerial exposure and estimated body temperature as tidal cycle timing progressively shifted over seasons.

Snails were disproportionately present in high shore areas when those areas were at seawater temperature, and minimized time spent at estimated body temperatures higher and lower than seawater (Fig. 6). 77.2% of snail body temperatures estimated from physical thermal models when snails were present in high shore foraging areas (T_s) were

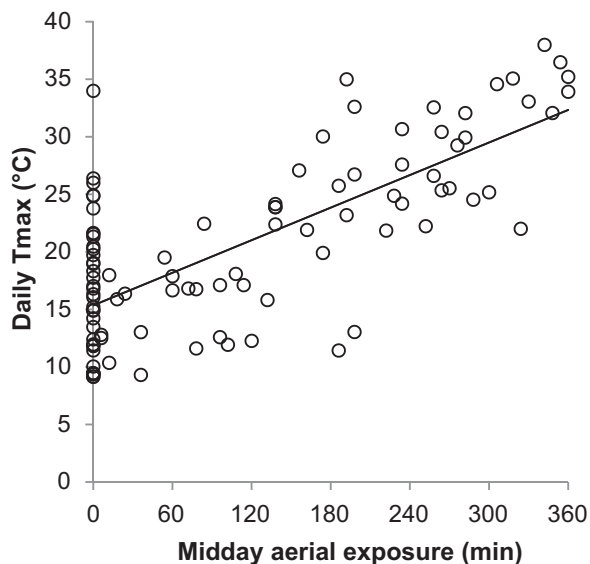


Fig. 5. Timing and duration of aerial exposure at low tide regulates daily maximum temperature.

Daily maximum temperature as a function of duration of midday aerial exposure due to low tide, defined as low tides occurring at solar noon \pm 3 h, over 14-week sampling period from August to November 2013 (97 days). Solid line shows linear fit, $R^2 = 0.533$, $p < 0.001$.

in the range 9–12 °C, whereas the mean percentage observed in 10,000 resamples of estimated body temperatures available in the environment (T_e) was 62.1% (95% CI 62.09–62.11) and maximum was 65.6%. Although on some days physical thermal model temperatures neared 38 °C, snails were not present in the adjacent antenna locations on these days. These detection absences in our continuous monitoring were confirmed with visual surveys. Snails were never detected in high shore areas above 30.75 °C, whereas the mean maximum temperature of 10,000 resamples of estimated body temperatures available in the environment (T_e) was 36.17 °C (95% CI 36.15–36.19). Similarly, snails spent no time below 3.90 °C, but the mean minimum of resampled T_e was 0.10 °C (95% CI 0.10–0.11).

4. Discussion

Nucella ostrina restricted foraging bouts in risky areas to days of the tidal cycle when midday aerial exposure was reduced. Snails moved into sun-exposed, high shore areas on some days, but were selective in their timing. This confirms that the same behavioral patterns that had been observed in manipulative experiments (Hayford et al., 2015; Vaughn et al., 2014) also occur in un-caged, natural settings, furthering the observations of *Nucella* spp. tidally-related movements in Europe (Burrows and Hughes, 1989), Africa (McQuaid, 1985), and North America (Spight, 1982), and their Australian Muricid relative, *Morula marginalba* (Moran, 1985). Regardless of causation, this behavior effectively minimized exposure to low tide conditions and the associated potential stresses. Behavior that consistently and effectively alters the thermal regime experienced by an organism will play a key role in determining individual and population fitness with climate change.

Tidal cycling may give snails a periodic environmental cue with broad stress-avoidance benefits. Though temperature was measured, this parameter often covaries with other stressors such as desiccation risk, UV, and salinity (Denny and Gaylord, 2010; Helmuth and Hofmann, 2001; Wolcott, 1973). It is unknown which, if any, of these correlated variables is the most important driver of snail response. The risk of these multiple stressors is suspected to have contributed to the development of avoidance of days and areas that experience a long duration of midday emersion. In fact, artificially warming low tide periods did not deter foraging behavior (Vaughn et al., 2014); suggesting that temperature alone is not the driving factor. Temperature could confound metabolic need and oxygen availability, however, *N. ostrina* is likely to respire aerobically during low tide as is seen in the Atlantic congener *Nucella lapillus* (Innes and Houlihan, 1985). Which-ever factors are drivers, it is clear that they are exacerbated by longer daytime aerial exposure. The observed behavior may be due to a circadian-like rhythm tuned to tidal cycling as has been seen in the gaping

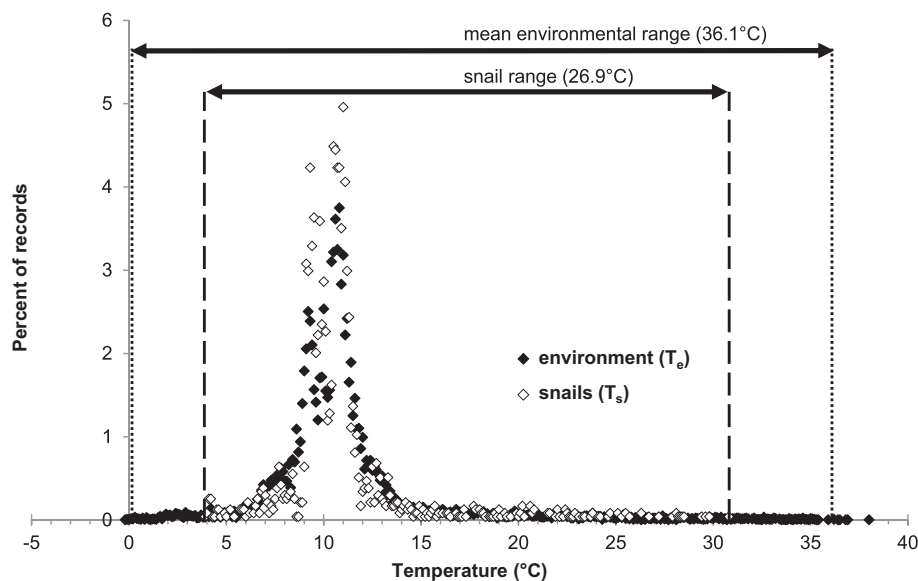


Fig. 6. Temperature experienced by snails.

Distribution of environmental temperatures (aerial and aquatic combined) measured every 15 min over 14-week sampling period from August to November 2013 by physical thermal models (T_e , black markers, $n = 19,200$) compared to the subset of temperatures experienced by snails foraging in high shore areas (T_s , white markers, $n = 2343$). Dashed lines mark the minimum (3.9 °C) and maximum (30.8 °C) temperatures experienced by snails. Dotted lines mark the mean minimum (0.1 °C) and maximum (36.2 °C) temperatures of 10,000 resamples of environmental data. Snails experienced a disproportionate amount of time at seawater temperature (9–12 °C, 77.2%).

of clams (Garcia-March et al., 2008) and the movements of horseshoe crabs (Chabot and Watson, 2010).

Despite variation in high shore *N. ostrina* abundance that coincided with duration of midday aerial exposure, a significant two-week periodicity was not observed in this study. This could in part be due to the seasonal switching of tidal regime from midday low tides during summer to midnight low tides during autumn. As the autumn season progressed, we observed an increase in the presence of *N. ostrina* during relative temperature spikes, however, these maxima did not exceed 25 °C and were therefore unlikely to be stressful. The benefit received by correctly selecting the days of the tidal cycle to forage and the cost of selecting the wrong days would likely both have lessened as maximum air temperatures decreased in the autumn. After September 11, 2013, thermal models did not record a single estimated body temperature that exceeded the lethal temperature for late summer/early autumn populations in Puget Sound, WA (34 °C, Bertness and Schneider, 1976, Hayford unpublished results).

The fluctuation of snail distribution suggests that surveys of *N. ostrina* abundance on exposed intertidal shores are very likely to yield inaccurately low numbers except on the days of the tidal cycle with cool, dark tides—those that occur at night or in the early morning and are traditionally least likely to be sampled by researchers. Thus, there is a discrepancy between conditions that are preferential for human observations and those that are preferential for organisms attempting to thrive in a dynamic habitat. It is important to keep this behavioral difference in mind when designing and interpreting field surveys to avoid human bias (Chapman, 2000). While this point is obvious in some animals, such as nocturnal species (Chelazzi et al., 1983; Jaberg and Guisan, 2001), this study shows it may apply to many cases where the critical elements of microclimate periodicity may be less apparent.

Although surveying only some days of the tidal cycle is likely to cause errors in population estimations, surveying daily only at low tide (and not during high tide) will yield an accurate picture of *N. ostrina* foraging behavior. This was also observed in the whelk predator *M. marginalba* (Moran, 1985), but not with grazing snail species (Hutchinson and Williams, 2003; Taylor et al., 2017). Unlike some Crustaceans (Chabot et al., 2004; Naylor et al., 1971), *N. ostrina* did not generally migrate into and out of high shore areas during one high tide. Over the 14 wk. period of observation there were only two incidents of an individual crawling onshore with the incoming tide and retreating within 2 h when the tide receded. While food may have been consumed during this journey, it could not have been a large amount due to the slow rate of consumption in this animal (mean 5.3 h per average-sized

barnacle, Emlen, 1966). Therefore, all substantive prey consumption was conducted during periods of time where the predatory snail was exposed to low tide aerial stresses for at least a portion of the foraging bout. Although some grazing snails move up and down shore in concert with the quickly-changing tides to feed in desirable conditions (Little, 1989), grazers in algae-rich areas capture energy incrementally. The high initial investment of prey handling time suggests that abandoning foraging bouts soon after initiation in response to changing tides would be energetically costly for predatory carnivorous snails (Burrows and Hughes, 1991).

Snails use two types of refuges to avoid exposed high shore areas during periods of stressful conditions: microclimates such as cracks in the rock and retreats lower on shore. The RFID method of tracking allowed better detection of the use of refuges; individual snails were found in locations where visual search was difficult and may have prevented identification of visual markers. Tagged snails were detected deeper in cracks than could be found by visual search alone. Importantly, organisms could be located and identified without interfering with their location and behavior. While tags may inhibit the ability of snails to fit into the smallest cracks, no other interference with their natural behavior was observed. We did not test whether the addition of tags altered snail behavior by changing hydrodynamic forces, heating rates, or ability to move. Because we observed similar trends between low tide surveys (tagged and untagged snails), remote tracking (tagged snails), and previous manipulative experiments (e.g. Hayford et al., 2015), we concluded that the effect of RFID tags on *N. ostrina* behavior was less than the effect of tidal cycle. These and other physical effects should be considered when designing a study using RFID tags.

Small scale habitat variability can determine evolutionary trajectories of animal populations (Dowd et al., 2015). This may be of elevated importance for slow organisms. Organisms can benefit from heterogeneity in environments where they can move to avoid stressful temperatures or thermoregulate to increase digestive efficiency (Caillon et al., 2014; Coggan et al., 2011; Lathlean, 2014). The range of motion of a snail is limited to a few meters per day and to submerged or moistened rock. If there is a high abundance of refuges created by microtopography, the energy expended to travel from thermal refuge to food and back could be greatly reduced (Fairweather et al., 1984; Sears et al., 2011, 2016). Similarly, a steep substrate slope, with abrupt changes in tidal water levels compared to a shallow slope, could enable movements between low and high shore areas for slow-moving animals. Therefore, a greater abundance of *N. ostrina* or other slow mobile intertidal invertebrates on substrates with higher heterogeneity

(Chappon and Seuront, 2011b; Gosselin and Bourget, 1989) and greater interaction strength between mobile predators and their sessile prey in thermally variable areas would be predicted.

Thermoregulation in slow-moving animals may be achieved over longer timescales than for fast-moving animals, and may depend on environmental cues that recur at known intervals rather than in response to continuous temperature sensing. An avoidance of high shore areas by *N. ostrina* on days that reached thermal extremes was observed, but not a clear selection of an optimal body temperature. A more precise understanding of *N. ostrina* performance across body temperatures is needed to evaluate possible benefits of the disproportionate amount of time spent at 9–12 °C (Hertz et al., 1993). Conditions that change rapidly require rapid movement if an animal is going to take advantage of abiotic shifts. Optimization may be physically impossible if the speed of an animal does not allow it to travel at a scale that is spatiotemporally beneficial. Repeated evidence that *N. ostrina* behavior is reducing risk of exposure to extreme conditions (Carrington and Kull, 2011; Hayford et al., 2015; Vaughn et al., 2014) suggests that risk avoidance, not optimization, may be the primary factor determining the thermal environment that slow intertidal invertebrates select. This conclusion was also reached in foraging behavior studies of the sea star *Pisaster ochraceus*, another slow intertidal predator (Monaco et al., 2015).

This two-part approach to estimating operative body temperature—radio tracking and physical thermal modeling—has been effective in organisms that cannot be constantly measured, for example, because they are too small for traditional telemetry, as in *N. ostrina*, or because they actively remove markers, as in the sea star *P. ochraceus* (Monaco et al., 2016). While estimates of organismal temperature are limited to the relatively low proportion of time that organism is present in targeted areas, this method allows identification of the upper bounds of body temperature a small organism experiences. Temperature extremes can provide a more accurate prediction of organismal stress and performance than average temperature experienced (Kingsolver et al., 2015), in part because temperatures may fluctuate above critical thermal limits while mean temperature remains within an organism's operating range (Camacho et al., 2015; Rezende et al., 2014).

Increases in air temperature due to climate changes are unlikely to negatively affect *N. ostrina* directly—it simply isn't present in the times and places where temperatures are extreme and it effectively avoids operative body temperatures near its lethal threshold. On the whole, this snail experiences moderate body temperatures well within its tolerable range. Overall increases in air and water temperature could alter the energy budget of this organism either negatively or positively, depending on how close normal operative temperature is to optimal temperature (Martin and Huey, 2008). For example, higher water temperatures lead to higher foraging rates, which may exceed the value of energy ingested from prey items. Increased metabolic demand could lead to elevated predation during times that are low risk for over-exposure (Yamane and Gilman, 2009). This may cause increased predation pressure on barnacles in pulses of feeding that occur during tides favorable for snails, leading to a potential shift in timing and magnitude of interaction strength between snails and their barnacle prey and possibly negative indirect effects on *N. ostrina* as its prey population declines. This example, and other ways in which spatiotemporal variability of temperature affects species interactions, should be focal in studies addressing the impact of climate change on intertidal communities as variability may influence ecological release and fitness benefits of population shifts (Buckley et al., 2013; Gilman et al., 2010).

5. Conclusions

The snail *N. ostrina* in uncaged, natural populations follows predictable changes in the tidal cycle, taking advantage of high shore food sources during times of low risk of exposure to damaging air temperatures and associated aerial stresses. Continuous tracking confirmed

that observations limited to low tide give a comprehensive snapshot of snail behavior throughout high and low tidal cycling. This evidence is consistent with prior experimental observations (Hayford et al., 2015; Vaughn et al., 2014) that *N. ostrina* selectively forages in places and at times that minimize aerial exposure and exposure to lethal microclimate conditions. Reference to the two-week tidal cycle is therefore critical to designing accurate surveys to estimate snail densities. The behavior of this slow-moving species in a highly fluctuating habitat effectively reduces thermal risk. This ability to thermoregulate using temporal cues that may be non-intuitive to researchers may significantly change the expected response of this and similar species to climate change.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.jembe.2017.12.005>.

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